Lecture 9 - Locomotion I: Flight

I. Powered flight has evolved independently many times in animals, but only once in mammals. It always involves a flight membrane and a support structure.

   A. Insects - membranous sheets of chitin supported by veins.
   B. Pterosaurs - skin membrane supported by single digit (4th).
   C. Birds - feathers, supported by limb bones and reduced 2nd & 3rd metacarpal and digit.
   D. Bats - skin membrane supported by the 2nd through 5th digits.
      Note how elongated the digits are.

II. Regardless of what the flying object is, the basic aspects of aerodynamics are the same.

   A. Flight involves overcoming the force of gravity, or generating lift.

      Lift relies on laminar flow, parallel movement of air streams (as opposed to turbulent flow).

      The principle is the same whether we’re addressing a bat or an airplane and involves an airfoil. They are usually asymmetric in cross-section.

      When the onrushing stream of air is split, some passes above and some passes below.

      The air that passes over the top of the air-foil accelerates, and moves faster than the air that passes across the lower surface: \( V_{\text{Upper}} > V_{\text{Lower}} \).
      This difference in velocities is critical.

      B. Bernoulli’s Theorem:
      \[
      P = C - \frac{dV^2}{2}
      \]

      \( P \) is air pressure, \( C \) is a constant, \( d \) is the density of air, and \( V \) is velocity

      Therefore, the higher velocity, the lower the air pressure and the fact that the airstream is moving faster across the top of the wing results in higher air pressure on the wing below than above. This differential in pressure is called lift, and when the magnitude of lift is greater than the force of gravity acting on the object, flight is achieved.

      \[
      \text{Lift} = P_{\text{(Lower)}} - P_{\text{(Upper)}}
      \]

      The magnitude of lift is dependent on the differential in \( V \), the speed with which air passes along airfoil. This differential increases with flight speed, so it’s more difficult to maintain flight at low speeds. For example, a plane has to accelerate to take off.
III. This is particularly important to flight in bats because, for the most part, they’re slow fliers.

There is variation in flight speed (look at 3 species we saw in lab):

- *Myotis lucifigus* - 20 mph
- *Eptesicus fuscus* - up to 40 mph
- *Tadarida brasiliensis* - up to 60 mph

But most bats are slow fliers, more like *Myotis*, and slow flying is probably the ancestral condition. Bats generate lift at low flight speeds.

A. Bats deal with generating **lift at low flight speeds** in a number of ways.

1. One is to increase the curvature of the upper surface – **camber**.

   The nature of the airfoil in bats is a little different than a plane; it’s a thin airfoil, and the shape can be modified. The skin in the patagium is thinner than typical and has elastin bundles running along the wing and there are up to 5 intramembranous muscles (Chaney et al. 2017. J. Anatomy, 230:510).

   As increase curvature → increase the differential in speed of airflow across upper surface relative to lower surface → increase lift.

2. Another is to increase the **angle of attack** - an airfoil coming at an air stream edge-on generates less lift than one that is inclined slightly. Again, this is because of the difference in distance that the split air stream travels.

3. A third relates to wing size and shape.

   a. **Wing loading** - Body weight / surface area.

      In general, the lower the wing loading, the easier it is to overcome the force of gravity.

      Bats typically have low wing loadings

      |                | Body Weight | Surface Area | Wing Load |
      |----------------|-------------|--------------|-----------|
      | **House wren** | 11.0 g      | 48.4 cm²     | 0.24 g/cm²|
      | **Glossophaga**| 10.6 g      | 99.3 cm²     | 0.11 g/cm²|
      | **Myotis**     | 4.2 g       | 67.6 cm²     | 0.06 g/cm²|

   b. **Aspect ratio** - shape of the wing - length / width
Low aspect ratio wings are better for slow maneuverable flight. Remember, Artibeus is a phyllostomid bat that eats fruit and forage in forests.

High aspect ratio wings are better for rapid flight. Tadarida is a molossid bat that you saw in the lab that forages in the open.

4. Another is a phenomenon called leading-edge flaps. At low flight speeds, there is a tendency for laminar flow to break down. The next time you’re on a plane check out the front of the wings on take-off. Leading-edge flaps promote laminar flow at low speeds.

Bats do all of these things. Slow flyers tend to have higher angles of attack, higher camber wings, and larger surface area wings with low aspect ratio.

B. Parts of a bat wing contribute differently to flight.

- Propatagium - between shoulder and wrist
- Dactylopatagium brevis - between first and second digits
- D. minus - between second and third
- D. longus - between third and fourth
- D. latus - between 4th and 5th
- Plagiopatagium - between 5th digit and the hind limb
- Uropatagium - between the two hind limbs

IV. So far we’ve only been talking about lift, but unlike in an aircraft, the wing also has to generate thrust.

A. Wing-beat cycle.

1. Down-stroke is the power stroke. It is powered by three muscles: pectoralis subscapularis serratus

2. One part of the wing in particular has been implicated in generating thrust.

Dactylopatagium longus. This is not well braced, so during the down-stroke, this segment of the wing lags above the rest of the wing. As the down-stroke finishes, the front of the D. longus is much lower than the back; this has the effect of forcing air backwards. This is what generates thrust. It is also likely that the D. latus has some thrust generating function as well.

3. The function of the other portions of the wing during the down-stroke.
Propatagium, D. brevis, and D. minus serve as leading edge flaps.

Plagiopatagiun is actually very well-supported by the 5th digit and the hind limb. It serves as the main airfoil.

This allows it to maintain both its camber and angle of attack throughout the down-stroke and therefore it is the primary lift generator.

The Uropatagium is not present in many bats, but it serves for steering, and in many insectivorous forms, is used as a net to catch insects in while flying.

4. The up-stroke is the recovery stroke in most forms.

The wing is partially closed

There are muscles that function during the upstroke, but these are greatly assisted by air pressure - so to some degree the upstroke is passive.

There’s a great deal of variation in the manner in which the up-stroke is stopped.

Shoulder-locking mechanism is formed by the greater tuberosity of the humerus.

In molossids, the really fast fliers, the situation is as I’ve shown in the slide.

In vespertilionoids, the greater tuberosity is also well developed, and acts as a locking mechanism.

In phyllostomids (and megabats, Pteropodids), there is only a moderate expansion of the greater tuberosity.

There are a few groups, such as the family Emballonuridae, with no expansion of the greater tuberosity, and no shoulder locking mechanism. The upstroke is stopped entirely by muscular contraction.

The nature of the shoulder locking mechanism is used to divide the families of microbats into 4 superfamilies.

V. Some other skeletal adaptations to flight.

A. Many bats have a keeled sternum - manubrium, the first segment.

B. Some have axial skeleton modifications.

Natalidae - very rigid axial skeleton that is formed by

1. Compressed thoracic vertebrae - not fused, but very tightly interconnecting
2. Fused sacral vertebrae and fused lumbar vertebrae.